Brain and Cognition **44,** 280–302 (2000)
doi:10.1006/brcg.2000.1231, available online at http://www.idealibrary.com on IDEAL®

Neural Representation for the Perception of the Intentionality of Actions

T. Jellema, C. I. Baker, B. Wicker, and D. I. Perrett

School of Psychology, University of St. Andrews, St. Andrews, Fife, Scotland, United Kingdom

Published online August 15, 2000

A novel population of cells is described, located in the anterior part of the superior temporal sulcus (STSa, sometimes called STPa) of the temporal lobe in the macaque monkey. These cells respond selectively to the sight of reaching but only when the agent performing the action is seen to be attending to the target position of the reaching. We describe how such conditional selectivity can be generated from the properties of distinct cell populations within STSa. One cell population responds selectively to faces, eye gaze, and body posture, and we argue that subsets of these cells code for the direction of attention of others. A second cell population is selectively responsive to limb movement in certain directions (e.g., responding to an arm movement to the left but not to an equivalent leg movement or vice versa). The responses of a subset of cells sensitive to limb movement are modulated by the direction of attention (indicated by head and body posture of the agent performing the action). We conclude that this combined analysis of direction of attention and body movements supports the detection of intentional actions. © 2000 Academic Press

INTRODUCTION

This article describes the response properties of several distinct but interrelated cell populations within the anterior part of the superior temporal sulcus (STSa), a high-level visual-processing area within the temporal cortex of the macaque monkey. The term STPa applies to the upper bank of STSa, which receives polysensory input (Bruce et al., 1981). Since we recorded from both the upper and lower bank, we use the term STSa. Section I of this article investigates the properties of cells responsive to faces, eye gaze, and body posture. We argue that subsets of these cells show characteristics compatible with the notion that the cells code for the direction of attention of the per-

We thank Dr. L. Fogassi for drawing our attention to the interaction between attention and action in the control of cell responses. T.J. is supported by HFSP, C.I.B. by St. Leonard's College and the University of St. Andrews, and B.W. by MNESR.

Address Correspondence and reprint requests to T. Jellema, University of St. Andrews, School of Psychology, St. Andrews, Fife KY16 9JU, Scotland, United Kingdom.

0278-2626/00 $35.00

ceived individual. Section II focuses on cells responsive to limb movements or actions, in particular reaching movements with the hand and arm. The cell populations in Sections I and II have been reported previously (e.g., Perrett et al., 1985a, 1985b, 1989) and are here confirmed by new data. Section III describes novel observations on a small number of cells whose response characteristics can be understood best as resulting from a combination of the characteristics of the cell classes described in Sections I and II. These cells respond to the sight of reaching but responses are conditional on the direction of attention of the agent performing the reaching. We propose that such combined analysis of direction of attention and actions makes the cell populations in STSa of the macaque suited to a role in inferring the intentionality of animate actions on the basis of high-level visual information.

Each of the three sections contains background, results, and discussion. We first present the general methods of experiments before providing a more detailed background to the distinct classes of cell.

METHODS

Spike activity was recorded from single neurons in STSa in awake, behaving, rhesus macaque monkeys (*Macaca mulatta*). The experiments were performed under appropriate UK Home Office Licence. A detailed description of the recording techniques can be found elsewhere (e.g., Perrett et al., 1984, 1985a; Oram & Perrett, 1996). A summary of the methods follows here.

Recording

A recording chamber was implanted under pentobarbitol (Sagatal) anesthesia (with full sterile precautions; see Perrett et al., 1985a for details). Spikes were recorded with glass-coated tungsten microelectrodes. Amplified and filtered spikes were sorted using a threshold voltage window and then captured (CED1401, Cambridge Electronic Design, UK) and fed to a PC for analysis. The raw spike signal was recorded on one audio track of a HiFi videotape recorder which simultaneously recorded the stimulus events (from the subject's perspective) through a video camera with a wide-angle lens. Eye movements were recorded during testing with a second (infrared sensitive) video camera mounted on the side of the primate chair. The signals from the two cameras were integrated (Panasonic VHS video mixer, WJAVE7) or synchronized with a time-code-generator and frame-counter (VITC Horita VG50) and recorded separately. Recording of the subject's eyes allowed trials on which the subject failed to attend to the stimuli to be discarded from the analysis.

Testing Procedures

Each cell was first tested ''clinically'' for its responsiveness to various movements (reaching, walking) and static postures of the experimenters (different head and body views with different gaze directions). Cells which could be broadly categorized in this way were subsequently tested using formalized protocols in which the stimuli were presented either live, on video, or on slides, in a computer-controlled quasirandom order, with 5–10 repetitions per condition. Objects available in the lab such as chairs, trays, and food were used as control objects. Stimuli were either presented from behind a fast rise-time liquid crystal shutter (aperture 20 by 20 cm at a distance of 15 cm) or without the shutter to avoid narrowing the scope of view of the subject.

Where testing involved investigation of attention and reaching direction, the experimenter sat on a chair 1.5 m in front of the subject and reached with his left or right arm in various directions, including toward the subject and up-downward. The reaching movement took about 1 s to complete. Simultaneously, the experimenter either paid attention toward his final hand position or looked away from his hand during the time the action was performed. Attention was paid by means of directing the eye gaze and rotating the head and upper body appropriately. The site the hand reached for was always located between 1 and 2 m from the subject.

Analysis

Off-line spike sorting was done using Spike2 (Cambridge Electronic Design, UK) when appropriate. When stimuli were presented from behind the shutter, spike counts started 100 ms after the shutter became transparent—corresponding to the average latency observed for cells in STSa (Oram & Perrett, 1996)—and lasted for 1 s, unless otherwise indicated. Cell responses were analyzed using ANOVAs (both online—to guide subsequent investigation—and offline) and Newman–Keuls post hoc tests (level of significance: $p < .05$).

Cell localization

At completion of each recording track, frontal and lateral X-ray photographs were taken with the electrode still in place to locate the electrode and the recorded cells with respect to specific bone landmarks (most notably the posterior clinoid process and the sphenoid bone; Aggleton & Passingham, 1981). During the final experiments, electrolytic lesions were produced at strategic locations by passing cathodal current (40 μA for 40 ms) through the tip of the electrode at the site of recording. The subject was sedated with Ketamine-HCl and killed with an overdose of barbiturate anesthetic. Transcardial perfusion was performed with buffered saline followed by paraformaldehyde (4%). The brain was removed and allowed to sink in increasingly concentrated sucrose solutions. Coronal sections (25 μm) were cut on a freezing microtome every 250 μm through the areas of interest, photographed, and stained with Cresyl violet. By aligning the X-ray photographs with the histological sections, cell locations could be determined with an accuracy of about 1 mm. All cells included in this report were found to be located within the banks of STSa, between 19 and 10 mm anterior to the interaural plane. A histological reconstruction of the locations of the various cell types described in this article is shown in Fig. 1 for one monkey.

I. CELLS IN STSa THAT CODE THE DIRECTION OF ATTENTION OF OTHERS

The temporal lobes of the monkey brain, and, especially, STSa are renowned for the presence of cells with highly complex visual properties, responding to the sight of animate objects and elaborate shapes. Gross, Rocha-Miranda, and Bender (1972) made the first startling finding of such cells that responded selectively to, for example, the sight of a monkey's paw. Subsequent work in STSa revealed populations of cells selective for the sight of faces (Bruce et al., 1981; Perrett et al., 1982). Though highly sensitive to complex shapes, these cells often appear to generalize shape selectivity across changes in various other stimulus properties such as size, retinal posi-

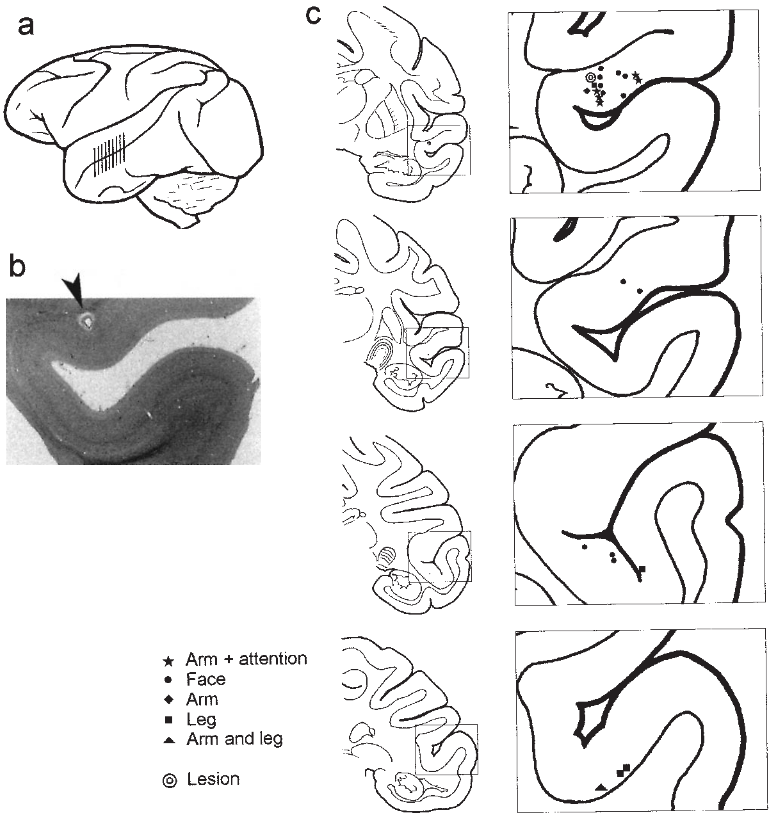

FIG. 1 Anatomical distribution of the different cell types within the anterior part of the superior temporal sulcus (STSa). (a) View of the left side of the macaque brain. The area where recordings were made was located in the upper and lower bank and the fundus of STSa between 19 and 10 mm anterior to the interaural plane (indicated by vertical bars). (b) A marker electrolytic lesion (arrow), made through the tip of a recording microelectrode, is located within the upper bank of STSa (Nissl-stained coronal section through STS). Cross-correlation of this lesion site with X radiographs of the positions of the recording microelectrodes allowed the recorded cells to be localized. (c) The left column shows coronal sections of the left hemisphere taken at respectively 17, 15, 13, and 11 mm anterior to the interaural plane. The boxes around the STSa are enlarged in the right column to reveal the positions of cells belonging to the different populations described in this study. The key to cell types sensitive to limb movement, face view, and combined reaching and attention direction are given in the box on the lower right. Each of the boxes contains cells located within an imaginary 2-mm-thick slice, which extends 1 mm into either side of the section shown along the anterior–posterior axis. Thick line, cortical surface; thin lines, edge of gray matter.

tion, orientation, and the species of face (human or monkey) and cues such as luminance and color (e.g., Perrett et al., 1984, 1989; Rolls & Baylis, 1986).

One of the most salient features of many of the ‘‘face’’ cells in STSa is that their response is selective for a particular view of a head (some respond only to the front view, others only to the left profile view and so on), while only a minority of them respond to all possible views of a head (Perrett et al., 1985a, 1991; Hasselmo et al., 1989). Likewise, particular views (or orientations) of other body parts, or of the whole body, evoke selective responses among STSa cells (Wachsmuth et al., 1994). The responses to faces have largely been interpreted as having a role in the recognition of faces as a class of objects or as belonging to individuals. Indeed, there is evidence that subpopulations of cells responsive to faces are sensitive to individual differences between faces (Baylis et al., 1985; Perrett et al., 1984, 1989, 1991; Young & Yamane, 1992).

The cells responsive to faces and bodies may not, however, have as an exclusive function the recognition of individuals. For instance, the responsiveness to just one view or orientation of an animate object may have a function in understanding an action sequence from momentary postures that constitute key components of that action (Byrne, 1995; Perrett, 1999). Another, particularly potent, use of view selectivity could be to infer the direction of attention of others (Perrett et al., 1992). Thus, a cell responding to the left profile but not to the right may code for the abstract notion of ‘‘attention directed to the observer’s left’’ instead of the more literal coding for the geometric characteristics of the left side of the face. The finding that cells coding for the frontal face view are most frequently encountered may then reflect the importance of attention being directed at the observer in social interactions. The visual information arising from body cues appears to contribute to cell sensitivity in a way that is consistent with the cell’s role in analyzing the direction of attention. For example, cells tuned to the left profile view of the head are often additionally tuned to the left profile view of the body (Wachsmuth et al., 1994). Thus such cell responses could signal that an observed individual is attending in a direction to the observer’s left.

The direction of another individual’s head or body may not always be a reliable index of where that individual’s attention lies. Gaze direction seems a better guide in this respect and gaze may therefore also be expected to affect STSa cell responses. Cells conjointly sensitive to gaze direction, head view, and body posture are capable of utilizing very different types of visual information, yet all of the information to which the cells are sensitive is compatible with the same conceptual interpretation of another individual’s direction of attention. In circumstances in which the direction of gaze of another individual is not clear, for example, when the eyes lie in shadow, then the head (and body) angle may provide useful backup information. Cells showing combined sensitivity to head view and gaze direction are therefore capable of signaling the direction of another individual’s attention under a variety of different viewing conditions (Perrett et al., 1992).

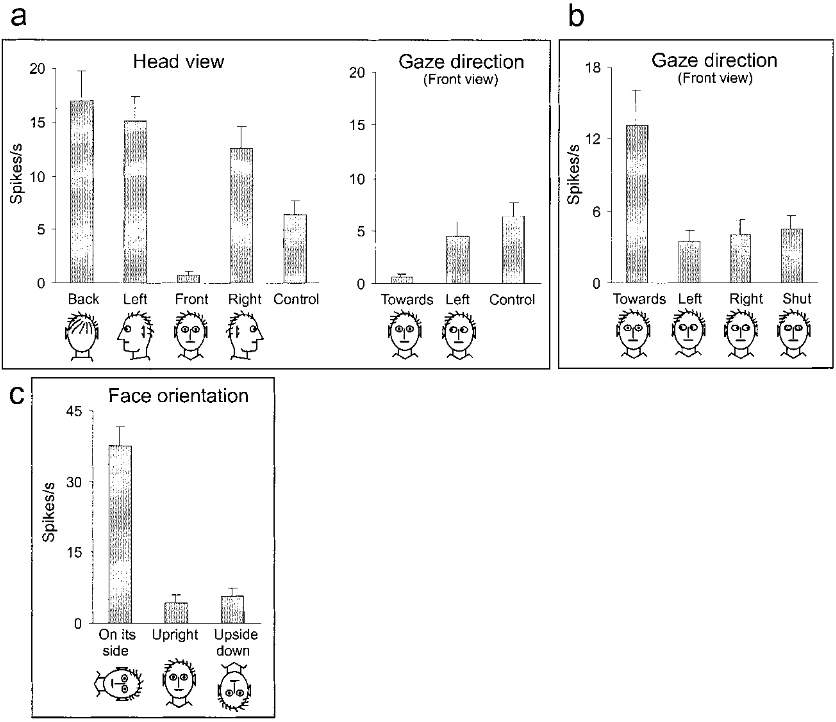

FIG. 2 (a and b) Two cells responsive to faces that may code for a perceived direction of attention. (a) Cell coding for attention directed away from the subject. (Left-hand side) The mean response ($+SE$) to the frontal face was smaller than to all other head views ($p < .0005$) and control objects (i.e., no person in view) ($p < .05$). [Overall effect of conditions, ANOVA: $F(4, 45) = 12.0$, $p < .000001$, $n = 10$ trials in each condition]. (Right-hand side) Switching the gaze direction of the stimulus face from eye contact (''Toward'') to gaze away from the subject (''Left'') removed the inhibition for the same cell ($p < 0.5$). [ANOVA:$F(2, 27) = 11.8$, $p < .0001$, $n = 10$]. (b) Cell coding for attention directed toward the subject. The head with frontal face and gaze directed at the subject (''Toward'') produced a significantly larger response than an identical head but with gaze directed to the left or right or when the eyes were shut ($p < .005$ for each comparison with ''Toward''). [ANOVA: $F(3, 16) = 7.2$, $n = 5$]. (c) A cell responsive to faces whose behavior cannot be explained as coding for a direction of attention. An isomorphic change in the orientation of the face produces a dramatic change in the response magnitude although the direction of attention remains focussed onto the subject ($p < .0005$). [ANOVA:$F(2, 12) = 46.5$, $p < .000002$, $n = 5$]. The stimuli in a and b consisted of live presentations of the experimenter's face, while the stimuli for c were 2D slides of a human face.

For example, the cell illustrated in Fig. 2a was inhibited by a frontal face looking at the subject but responded vigorously to the right and left profiles and to the back of the head (live presentation of the experimenter's head). When, however, the gaze of the frontal face was directed away from the subject to the left or to the right (the latter is not shown), the inhibition to the frontal face was lifted and the spiking frequency was no longer different from the spontaneous level (i.e., with no person in view) (Fig. 2a, right-hand side). This latter effect could be repeated very reliably by alternating between the two eye gaze directions. A plausible interpretation is that this cell contributes to the coding for attention directed away from the subject. For this cell, this information about the direction of attention is obtained from two different visual cues: averted eye gaze direction and averted head views (including the back of the head where the eyes are not visible).

By contrast, the cell in Fig. 2b responded maximally when the gaze was directed at the subject and significantly less when gaze was directed away to the left or right (live presentation of the experimenter's face). The absence of gaze, that is, when the eyes were closed, also evoked a significantly smaller response than gaze directed at the subject. Sensitivity to eye contact worked equally well for the right profile view of the face. Eye gaze compatible with head direction (both directed to the right) gave no response, but subsequently switching the gaze direction toward the subject did produce a response (data not illustrated). The responses of this cell can be interpreted as contributing to the coding for attention directed at the subject. Thus, for the cells illustrated in Figs. 2a and 2b, both head view and gaze direction controlled the responses, though we do not know the relative importance of these two cues. For other cells it has been shown that sensitivity to gaze direction overrides sensitivity to head view in cases where these two cues are in conflict (Perrett et al., 1992).

Previous studies have emphasized the capacity for temporal lobe cells responsive to faces to generalize across retinal position (Perrett et al., 1989; Tovee et al., 1994). For the cell illustrated in Fig. 2b, sensitivity to attention direction also generalized from central to peripheral vision. The subject did not need to look at the stimulus face directly in order for the cell to respond to attention toward the subject. The response could equally well be evoked while the subject directed his eyes to a television screen in front of him and the experimenter's face was introduced (1 m away) 45° to the left of the screen without the subject switching his gaze toward the left.

Not all cells responsive to faces in STSa appear to signal attention direction. For about 40% of cells responsive to faces in the present and previous studies (e.g., Perrett et al., 1985a) it was found that the response to the optimal face view was not affected by changing the eye gaze direction or by closing the eyes. Conversely, leaving the gaze direction unchanged but changing the head view from the optimal view to an ineffective view usually did affect the responses. For these cells, head view controlled responses but gaze direction did not. Such cells may not be coding attention direction or at least are not coding it with multiple visual cues.

Another example of cell sensitivity to faces that is not consistent with an abstract coding of attention direction is provided by the cell responses illustrated in Fig. 2c. This cell responded to static slides of a frontal face on its side but stopped responding when the face was rotated in the picture plane to the upright or upside-down orientations. The cell showed the same selectivity for both human and monkey faces, whether they were shown on slides or live (only human faces). In this case, a radical change in the response of the cell was produced by a change in the orientation of the face, while the attention conveyed by the stimulus face remained invariably focused on the subject. We thus do not argue that coding for the direction of attention applies to all face cells in STSa but, rather, that coding for this more abstract concept is ''constructed'' within STSa, using the ''simpler'' characteristics of many face- and gaze-selective cells.

Thus, a cell coding attention to the right may pool excitatory inputs from three types of cell: (a) cells selective to gaze directed right but unresponsive to other parts of the right profile, (b) cells selective for the right profile head view but unresponsive to gaze right, and (c) cells sensitive to the right profile view of the body but unresponsive to visual cues from the head (e.g., Wachsmuth et al., 1994). Such a cell might also be influenced by inhibitory connections from further cell types responsive to eye contact as well as by other cells coding the frontal head view. With this collection of excitatory and inhibitory inputs the cell would signal attention right from a variety of cues giving priority to gaze over the rest of the head and to the head over the rest of the body.

In humans, the capacity to detect the direction of attention of others is well developed. Human infants from the age of 1–2 years already appear to comprehend the goal of the mother's gaze (head and/or eye orientation) and will direct their own gaze at the object fixated by the mother (Scaife & Bruner, 1975; Butterworth & Jarrett, 1991; Corkum & Moore, 1994). Baron-Cohen (1994) has argued that the detection of the direction of gaze could contribute to the forming of a ''theory of mind,'' since the inferred direction of attention can provide clues to what someone is thinking. Such a capacity is essential for social development and appears impaired in autism (Baron-Cohen, 1994; Leekam et al., 1997; Emery & Perrett, 1999).

Chimpanzees have been shown to possess the capacity to follow attention (Povinelli & Preus, 1995). The extent to which Old World monkeys are able to use information about the gaze direction of others still remains a matter of debate, despite the neurophysiological findings of cellular sensitivity to attention direction in macaques. For example, Anderson et al. (1996) report that macaque monkeys cannot be trained to use human gaze to locate hidden food. Recent behavioral assessments in our lab have shown that macaques do spontaneously utilize the direction of attention of conspecifics to orient their own attention (Emery et al., 1997). In these studies, film or slides are presented which contain a display monkey directing eyes, head, and body toward a specific location. Monkey subjects that observe such slides or film redirect the position of their own gaze to be congruent with the stimulus monkey. These studies show that monkeys use multiple visual cues and follow gaze direction or head view in preference to body direction (Lorincz et al., 1998). Thus the order of importance of cues to attention at the behavioral level parallels that seen at the cellular level.

II. CELLS IN STSa RESPONSIVE TO LIMB MOVEMENTS

Other populations of cells in STSa are selectively responsive to particular types of body movements and remain inactive to static images of the body. Specific types of body movement that are found to be processed include translation (linear displacement) and rotation (Perrett et al., 1985b; Oram et al., 1993). For some of these cells, the body as a whole needs to move in order to produce the response (Oram & Perrett, 1994, 1996; Oram et al., 2000). Other cells require only the movement of a specific part of the face or body, such as the mouth, eyes, head, torso, legs, arms, hands, and fingers (Perrett et al., 1985b, 1990a, 1990b; Mistlin & Perrett, 1990; Oram et al., 2000).

Usually the direction in which the movement is performed is crucial, e.g., the cell may only respond to movements away from the subject or only to movements to the left. A further complication is that often the particular view of the body interacts with the direction of motion in controlling responses. For instance, the cell may respond to the right profile of an individual walking to the right of the subject, but not to the left profile view moving along the same trajectory (i.e., walking backward), nor to the right or left profile views moving left (Perrett et al., 1985b; Oram & Perrett, 1994, 1996). What all of these STSa cells have in common is that they combine information about the form of the object with information about its movement. This form/motion selectivity seems to be a unique feature of many cells in STSa (Oram & Perrett, 1996).

Other STSa cells seem to have a more abstract function in that they are sensitive to the causal relationship between an action and the object or goal of that action (Perrett et al., 1989). Distinct populations of cells are tuned to different actions (tearing, reaching for, picking, walking to, picking up; Perrett et al., 1989, 1990b). For instance, cells may respond to the sight of a hand manipulating an object but not to the same manipulating action in the absence of the object, nor to just movement of the objects as if manipulated but with the hand out of sight. Furthermore, even when both hand and object movements are visible but the hand mimics the manipulating action just a few centimeters above the object, the cells do not respond (Perrett et al., 1989). This sensitivity of STSa cells to the spatial relation between the agent and the object of the action imbues the cells with the capacity to detect causal relations within actions.

We consider in more detail cells specifically responsive to *limb* movements. Such cells constitute about 6% of cells in STSa sensitive to body movements (Oram et al., 2000). We have studied 15 cells that responded

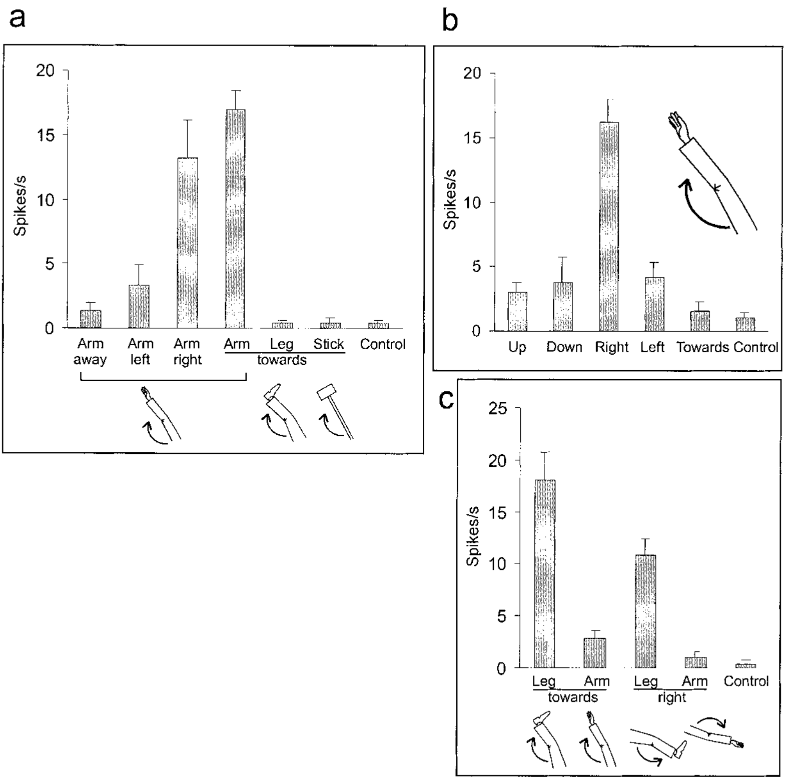

FIG. 3 Responses to the sight of limb movements. (a) The cell was activated by the sight of the experimenter extending his arm either toward the subject or toward the subject's right. Equivalent movements of the leg and a stick in the direction toward the subject did not excite this cell at all ($p < .0005$, each compared to arm toward).[ANOVA: $F(6, 38) = 34.5$, $p < .000005$; number of trials for each condition from left to right, $n = 5, 5, 5, 10, 5, 5, 10$]. (b) This cell responded selectively to an arm reaching to the subject's right ($p < .0005$ in all comparisons to ''Right''). [ANOVA: $F(5, 24) = 19.5$, $p < .0000$, $n = 5$]. (c) A different cell which responded much more to a leg extension than to an equivalent arm extension, both toward the subject ($p < .0005$) and to the subject's right ($p < .0005$). The cell preferred direction ''Toward'' above direction ''Right''($p < .005$).[ANOVA: $F(4, 20) = 26.7$, $p < .000005$, $n = 5$]. The ''Control'' condition consisted of a static person, which did not produce a response in any of the three cells shown (a–c).

selectively to arm movements and not to equivalent leg movements, 16 cells that responded selectively to leg movements and not to equivalent arm movements, and 5 cells responded equally strongly to both leg and arm movements. Such cells usually also exhibit direction selectivity. Figure 3 gives three examples of such cells. The cell in Fig. 3a responded specifically to the sight of an arm movement; equivalent movements made with a leg or with a stick failed to excite this cell. The arm and leg movements were directed to the same position (approximately 1.5 m above the ground and 1 m in front of the subject). For the cell illustrated, a reaching movement made with the left or right arm was equally effective. Reaching was effective when directed toward the subject or to the subject's right, but not when directed away from the subject or to the left. Leg and stick movements were ineffective in all directions.

Most cells responsive to arm reaching were found to be optimally responsive to reaching directed toward the subject. Some cells responded selectively to reaching in one direction away from the subject (e.g., to the subject's left) and remained silent to reaching toward the subject. An example of a cell of the latter category is given in Fig. 3b. This cell responded selectively to arm reaching to the subject's right and was significantly less responsive to reaching directed toward the subject, up, down, and to the subject's left.

Cells selective for limb movements can also be selective for limbs. One cell that responded to arm movements was found to distinguish the movements of the left and right arms. It responded to movements of the left arm to the left but did not respond to the right arm reaching in the same direction (to the left).

The cell shown in Fig. 3c responded vigorously to the sight of leg movement but hardly at all to an equivalent arm movement. Again, the cell was directionally sensitivity in that leg movement toward the subject was more effective than movement to the subject's right ($p < .05$). Leg movements directed away from the subject also failed to produce a response (not shown). Interestingly, cells specifically responsive to ''arm'' and ''leg'' movements could be found located very closely to one another. For instance, the two cells illustrated in Figs. 3a and 3c were located only 60 μm apart on the same recording track.

There are several visual cues to the difference between arm and leg movement and we have yet to establish which the STSa cells utilize. Cells may utilize the form of the limb (including the position of attachment on the body) to differentiate between limbs. We have found that some cells responsive to an arm movement are less responsive if the torso attached to it is not simultaneously visible.

Arm and leg movements differ in the kinematics of articulation. They, however, did not account for cellular selectivity in some cases. For instance, cells responsive to leg movement often remained unresponsive to arm movements even when they were made to simulate the trajectory and articulation of the effective leg movements. Moreover, cells responsive to arm motion but not to leg motion failed to respond to two sticks joined at one end made to articulate in the same manner as an arm.

One can ask what the function is of the visual coding for specific limbs moving in specific directions. Reaching in different directions has different consequences for the observer. For example, tactile contact with the subject will result only from movement toward the subject. Indeed, one population of STS cells recorded at more posterior locations (Mistlin and Perrett, 1990) has conjoint visual and tactile properties. Cells sensitive to the onset of tactile stimuli were found to be tuned to reaching toward the subject, whereas cells sensitive to the offset of tactile stimulation were tuned to movements of the experimenter away from the subject. Even among cells without obvious visual responses, it was possible to demonstrate the impact of ''expectations'' made between visual and tactile modalities. For cells responsive to tactile onset, tactile contact that could be expected because of the sight of preceding movements produced less of a response than unexpected tactile contact. Similarly, the responses of cells selective for the offset of tactile contact were reduced when the offset could be anticipated because the subject could see the experimenter withdrawing from contact. In this way, the sight of movements toward or away from the subject can be used to make predictions about impending events.

Movements directed away from the subject will also acquire particular meaning in a given context. For example, if a food tray is kept out of sight to the subject's right, then the sight of the experimenter reaching right can become salient, since this may bring the experimenter's hand to food, which is subsequently given to the subject. The significance of such events may account for the sensitivity of cells to the distinction between arm and leg movements. Arm movements bring the experimenter's hand to objects, which may then be picked up. The experimenter's leg movements do not result in objects being picked up. Even for monkeys, who are far more dextrous with their feet than humans, hands are used in preference to feet when reaching to retrieve objects. Foot movements are more likely to be made toward objects that are to be used for postural support or as an aid to locomotion.

In summary, to understand the nature of body movement it is a good starting point to differentiate between movements of the arm and leg and to specify the direction of those movements. Cell populations within the STSa appear equipped to do just that. Analysis of the position of cells sensitive to limb movements suggests a more posterior and ventral distribution compared to cells described in Section I that are sensitive to the face and gaze direction. Our sample is, however, small and cells responsive to faces can be found in clumps at several locations along the entire length of the upper bank of the STS (Harries & Perrett, 1991).

III. CELLS RESPONSIVE TO THE INTENTIONS OF REACHING ACTIONS

For a subset ($n = 7$) of the population of STSa cells responding to perceived reaching movements of the arm, it was found that the magnitude of the response could be influenced by the direction of attention of the agent performing the action (i.e., the experimenter). These cells were found at the same location as those responsive to the face and gaze direction described in Section I (Fig. 1). Figure 4 illustrates the behavior of one such cell. The reaching action evoked a pronounced response in this cell, provided the experimenter paid attention to the target position of the reaching (Fig. 4a, left, indicated by a horizontal bar labeled ‘‘reaching’’). Usually, the target position during testing was merely a position in the air, not obviously associated with a particular object.

When the experimenter made exactly the same reaching movement but paid no attention to his arm—by constantly looking away to either the left or right—the response was significantly smaller (Fig. 4b, left; $p < .001$). The direction of reaching was crucial: When the action was performed not in the direction of the subject but 45° to the left or right of the subject, the response was very much reduced and no longer significantly different from spontaneous firing levels. Attention of the performer congruent to such a reaching action did not enhance the response (Fig. 4c). The mean spike frequencies during the reaching action for each of the conditions are indicated in Fig. 4d.

The difference between the attended and unattended conditions was not confined to the actual reaching movement, but persisted in the subsequent phase during which the experimenter held his arm static in the extended position. These latter responses are shown at the right hand side of the panels in Figs. 4a–4c, indicated by bars labelled ‘‘extended.’’ The response to the static extended arm was evident for at least 7 s following the reaching movement (Fig. 4e). Throughout this period the response to the attended extended arm was significantly larger ($p < .005$) than the response to the unattended extended arm. In the unattended situation, the relatively weak response to the reaching movement quickly faded away once the arm had reached the static extended position.

Since the only difference in the visual stimuli between the attended and unattended conditions was the orientation of the head and gaze, we tested the response of the reaching cells to different views of the head (and body) without the arm reaching or being held extended. The stimuli thus consisted of static views of the experimenter, with the head oriented in different directions (gaze and head compatible). None of these stimuli raised the firing frequency of the cell significantly above its spontaneous level (Fig. 4f). For this cell, head orientation toward the subject produced the highest firing rate (mean: 3.4 spikes/s), but this was not significantly different to other head views and was much lower than the firing rates during reaching and arm extended with attention. The influence of gaze direction on its own was not investigated here.

The influence on the responses of the presence of an object, which formed the target of the reaching action, was tested in five cells of this population.

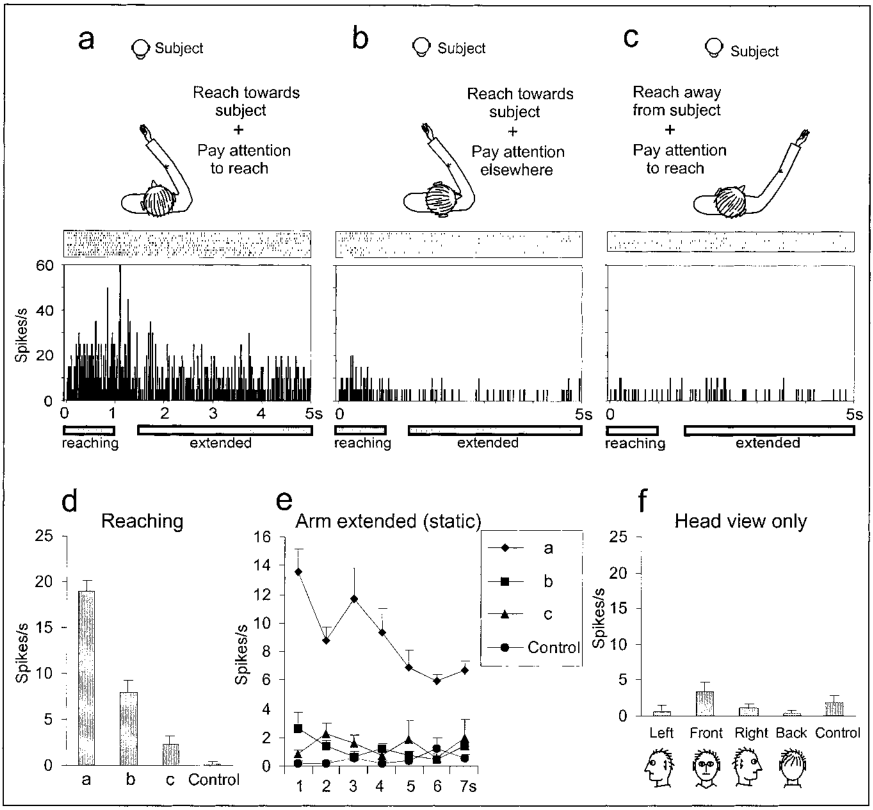

FIG. 4 The response to the sight of a reaching movement depends on the direction of attention of the performing agent. (a) The experimenter reaches his arm in the direction of the subject while constantly paying attention to his arm. The schematic drawings, at the top, show the experimenter and the subject (as seen from above) to indicate their relative positions. Peristimulus time histograms (bin width = 20 ms), with spike rastergrams on top, are shown. The reaching action itself causes a large burst, which continues at a slightly lower level during the subsequent period during which the experimenter holds his arm static extended while he continues to pay attention to it. (b) The experimenter performs an identical movement but looks continuously away. (c) The experimenter reaches 45° to the subject's left and attends in the same direction. (d) The mean ($+SE$) of the responses shown in a–c during the reaching action (duration, 1 s) are shown. ''a,'' Reach toward subject + attend to reach; ''b,'' Reach toward subject + pay attention elsewhere; ''c,'' Reach away from subject + pay attention to reach. ''a'' > ''b'' ($p < .0005$),''b'' > ''c''($p < .0005$).[ANOVA: $F(3, 29) = 46.8$, $p < .00001$, number of trials for each condition from left to right, $n = 10, 10, 8, 5$]. (e) The response to the attended, static, extended arm toward the subject remained significantly higher for at least 7 s than in the other three conditions ($p < .0005$, for each comparison)[ANOVA with time as a factor: $F(18, 150) = 3.0$, $p = .0001$]. (f) The responses to different head views were all relatively small, without significant differences between them. [ANOVA:$F(4, 20) = 2.1$, $p = .11$, $n = 5$.]

The object was food located on a tray 1.5 m in front of the subject. One cell showed a small but significant increase in firing rate in the presence of the food when the experimenter paid attention to it. Mere presentation of the food did not excite this cell. The responses of the other four cells were not affected by the presence of this target object. None of the responses was affected by the presence of an object in the experimenter's hand during reaching (a syringe containing juice).

We have only just begun to study this ''modulation'' of responses to reaching by the direction of attention but our initial findings suggest that the phenomenon may be widespread. We have tested nine reaching cells so far for the effect of attention. Of these, seven cells showed the attention-modulation effect during the reaching action ($p < .05$ for each cell), while two did not. For the seven cells, the mean response magnitude in the ''attended'' condition was more than twice that of the ''unattended'' condition. For four cells the preferred direction of the reaching movement was confined toward the subject (e.g., the cell in Fig. 4). For the other three cells the optimal direction was 45° to one side of the subject but directional tuning was broad and the cells were equally responsive to movements 0° or 90° to one side of the subject.

The prolonged response to the static extended arm when the action was accompanied by the attention of the performing agent (see Figs. 4a and 4e) was also observed in two other cells. Such prolonged responses are rare among STSa cells responsive to static or moving bodies and we do not yet understand their significance.

So far we manipulated the attention of the performing agent by changing the agent's head and gaze direction. Body posture provides another potential cue to the direction of attention (Perrett et al., 1992; Wachsmuth et al., 1994). The cell responses illustrated in Fig. 5 indicate that body posture can also contribute to the ''modulation'' of the response to a reaching movement. The cell responded maximally to the sight of the experimenter reaching toward the subject, while the experimenter's head and body were also directed toward the subject. The cell showed reduced responses to reaching when either the experimenter's head or the experimenter's body was rotated toward the subject's left. Two-way ANOVA revealed a significant main effect of head direction ($p < .005$) and a significant main effect of body direction ($p < .005$). In this case, the head and body had equal effects. When both head and body were rotated away, a further significant reduction in the response resulted.

One question to be addressed in future studies concerns the accuracy of coding for attention direction. Do STSa cells code the subtle difference between situations in which the agent's attention is focused precisely congruent with the direction of reaching and situations in which the agent's attention is only broadly compatible with the direction of the reach? Preliminary observations indicate that this might be the case.

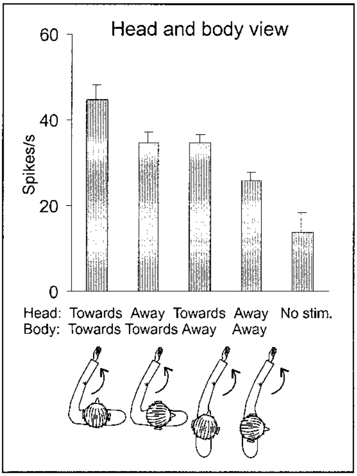

FIG. 5 Body view can also modulate the response to a reaching action. The experimenter reaches with his left arm in the direction of the subject. The reaching action evokes the largest response when both head and body view of the experimenter are directed toward the subject. A significant, equal, reduction in the response occurs when the reaching is performed with the head averted 90° away to the subject's left or when the head remains directed toward the subject but the body is rotated 90° away to the subject's left. When both head and body are rotated away, a further significant decrease results. Two-way ANOVA revealed a significant main effect of head direction [$F(1, 16) = 12.7$, $p < .005$, $n = 5$] and a significant main effect of body direction [$F(1, 16) = 12.7$, $p < 0.005$, $n = 5$], with no interaction between head and body [$F(1, 16) = 0.07$, $p = .79$]. In the ''Control'' condition the experimenter is not in view.

GENERAL DISCUSSION

We described the unique response characteristics of two distinct populations of cells located within STSa. The *first* population of cells responded to particular head views and gaze directions. We argued that a subset of these cells codes for the direction of attention rather than for the particular face view per se. Certainly, coding for the direction of attention is not a feature that applies to all face cells in STSa, but our findings are compatible with the idea that neuronal circuits in STSa play an important role in constructing the abstract notion of the direction of attention in others. Individual cells reported here possess response characteristics that put them in an ideal position to contribute to such a function.

The *second* population of cells, located within the same area of STSa, responded to reaching movements performed with the arm into a specific direction. The responses of a subset of these cells were affected by the direction of attention of the agent performing the reaching action.

We have reviewed evidence that populations of STSa cells responsive to the sight of the eyes, face, and body code the direction of another's attention both toward the observer and elsewhere in the environment. Specific subpopulations code attention in different directions, left, right, up, and down, with respect to the observer. Cells coding limb movements too exhibit a variety of directional tuning; some are tuned to reaching toward the observer, others to reaching to the observer's left, and so on. By combining the appropriate outputs of these two cell types it is possible to derive the third cell type described here with conjoint selectivity for reaching and attention in the same direction. In this manner it is possible to generate cells selective for reaching and attention to the observer's left and different cells selective for reaching and attention directed high up, and so on.

The significance of someone reaching toward an object while his/her attention is directed toward the same object clearly differs from an identical arm and hand action performed with attention elsewhere. In the former case one is likely to infer that it was this person's intention to reach out for the object in order to pick it up or make contact with it. In the latter case one may infer that the object was incidental to the arm extension. Crucial here is that information about the reaching action, such as its direction and the possible presence of a reaching goal, is linked to information about the direction of attention of the performer.

We propose that the information about the direction of attention ''modulates'' the responses of reaching cells such that the response magnitude of these cells reflects the intentionality of the action. The cells are selective for actions where the agent's attention is focused on the goal of the action. As such the cells can be seen as selective for movements of the agent which appear purposive and intentional.

There have been few behavioral studies of the capacity to distinguish intentional from nonintentional actions in nonhuman primates (Premack and Woodruff, 1978; Call and Tomasselo, 1998). The most relevant here is the study of Call and Tomasselo (1998), who compared the perception of intentional and accidental actions in seven chimpanzees, five orangutans, and 16 children (2 or 3 years of age). For intentional actions the experimenter looked at a target surface while placing a hand-held marker object on the surface of a box or while opening a hand to release the object onto the surface. For accidental actions the experimenter ''looked away from the surface'' and knocked the object on to the surface from an adjacent apparatus with an arm movement or by surreptitiously moving the apparatus. In the accidental condition the experimenter also made an expression of disapproval. Call and Tomasselo (1998) found that the 3-year-old children showed clear evidence of choosing a box marked by intentional actions. Collectively, the nonhuman great apes too showed evidence of preferentially following intentional actions, but the effect of intentionality was less consistent and, as for the 2-year-old children, was prevalent on initial blocks of trials.

This behavioral study provides evidence that nonhuman primates discriminate between intentional and nonintentional actions. It is relevant here that in the Call and Tomasselo (1998) study a major difference between intentional and unintentional actions was formed by the direction of attention of the agent performing the action; the experimenter demonstrated the intentional actions (in part) by attending to the goal of an action.

The advantages of being able to determine others' intentions from their actions are obvious. Among other things it allows the observer to quickly anticipate the nature of the future actions of the other individual (which may range from friendly and cooperative to hostile and threatening) and to adjust responses accordingly. It remains a moot point, however, whether nonhuman primates possess the ability to ''read the minds'' of others, i.e., to attribute mental states to others. The existence of at least some elementary form of mind reading in nonhuman primates is suggested by the reports of intentional deception (Byrne, 1995; Byrne & Whiten, 1988). Our working hypothesis is that the differences that exist between nonhuman primates and humans in the ability to attribute mental states to others are not fundamental but gradual, representing different points on a mind-reading continuum.

Other brain regions will undoubtedly contribute to the ability to attribute mental states, such as intentions, to others. One of the major output connections from STSa is to the amygdala (Aggleton et al., 1980). This area also contains cells responsive to the sight of faces, bodies, and their movement (Rolls, 1984; Leonard et al., 1985; Brothers et al., 1990). So far, research on amygdala function has focused on emotional expression, and cells within both the STS and the amygdala show sensitivity to facial expression (Rolls, 1984; Perrett et al., 1984; Hasselmo et al., 1989). The amygdala cells, however, have not yet been assessed for sensitivity to gaze and actions. Generally, the amygdala appears to be involved in linking sensory stimuli to particular emotional responses such as fear (Aggleton, 1993), possibly through classical conditioning (Wiener & Levine, 1992). In humans, amygdala lesions result in impaired judgement of gaze direction and facial expressions (Aggleton, 1993; Young et al., 1995). One can thus envisage a role for the amygdala in the assessment of the emotional significance of actions (including their intentionality) but this has yet to be investigated. Indeed Call and Tomasselo (1998) used the expression of disapproval as one cue to the difference between intentional and unintentional actions. Although the extent to which the amygdala is involved in processing the expression of disapproval is not clear (Phillips et al., 1997; Morris et al., 1996).

The premotor cortex shows striking similarities to the STSa in terms of the cells responsive to the sight of actions. The inferior area 6 of the premotor cortex can be subdivided into areas F4 and F5 (Rizzolatti & Gentilucci, 1988). Neurons in F5 are activated during specific motor acts performed with the hand or mouth, such as grasping, holding, and tearing. Cells with responses related to reaching movements of the arm are typically found in F4. The majority of the F4 neurons, and to a lesser extent the F5 neurons, are also activated by tactile stimuli and, in addition, by visual stimuli. Of relevance here, is the finding that cells in F5 that discharge during the execution of a particular action can also be excited by the sight of the same action. For example, a cell responding during the execution of a grasping action may also respond to the sight of another monkey or the experimenter grasping an object but not to the sight of different actions such as picking (Di Pellegrino et al., 1992; Gallese, 1996; Rizzolatti et al., 1996). These cells, called mirror neurons, thus constitute an observation/execution matching system and may, as such, enable the imitation of observed behaviors. Alternatively, the F5 cells could provide an internal representation of the observed action.

Thus the F5 mirror neurons and subsets of STSa cells comprise two systems for the visual detection of actions. The similarity between cells in both areas that code for perceived hand actions, such as, holding, tearing and manipulating, is quite striking (Perrett et al., 1989). In both areas, cells code for hand actions that are performed to achieve a particular goal rather than for simple movements produced by contractions of individual muscle groups. Thus subgroups of STSa and F5 cells code meaningful actions rather than arbitrary movements. There may be further similarities between frontal and temporal coding of actions. Of particular relevance was the observation of a single cell in frontal cortex that responded to the sight of an experimenter grasping an object when the experimenter was looking at the object but not when the experimenter looked away from the object (L. Fogassi, personal communication).

Gallese and Goldman (1998) suggested that the ‘‘action detecting’’ system in STSa could provide an initial ‘‘pictorial’’ description of the action that would then feed to the F5 motor vocabulary, where it would acquire a meaning for the individual. We agree that it is quite possible that the results of the high-level visual analysis of animate actions in STSa are fed forward to the premotor cortex, where they activate circuits comprising mirror neurons, which can, in principle, reproduce the perceived action.

A function of the mirror neurons might then be to complement the STSa description of the perceived action by adding information about the motor requirements of the action, which could not easily be obtained from purely visual features. When one observes an arm action performed by another, one is not only ‘‘aware’’ of the visually detectable characteristics such as the direction of the movement, the speed, and the shape of the arm and hand, but also of motor characteristics of the movement such as the force and the dexterity with which it is executed. These latter features may be better appreciated by simulating the execution of the perceived action internally. In this view the mirror neurons in the premotor cortex are an integral part of the perceptual system for perceiving and understanding animate actions. At a more speculative level, it has also been proposed that the mirror neurons are involved in the ability to ‘‘read’’ others’ minds. The cells may allow an observer to ‘‘experience’’ and understand an action performed by another through the observer’s ability to ‘‘simulate’’ the same action (Gallese & Goldman, 1998).

Clearly, determining the intention or purpose of a perceived animate action involves many cues, most of which are processed within the visual system, but the emotional system (including the amygdala) and, as argued by Gallese and Goldman (1998), the motor system, also contribute to the processing. The ability to determine others' intentions is thus likely to be a widely distributed function, involving many brain areas. The present article argues that the STSa plays an important role within this network in that it provides the neural substrate for the integration of high-level visual information about the particular perceived action with information about the direction of the attention of the performer of that action.

REFERENCES

Aggleton, J. P., Burton, M. J., & Passingham, R. E. (1980). Cortical and subcortical afferents to the amygdala of the rhesus monkey (*Macaca mulatta*). *Brain Research,* **190,** 347–368.

Aggleton, J. P., & Passingham, R. E. (1981). Stereotaxic surgery under X-ray guidance in the rhesus monkey, with special reference to the amygdala. *Experimental Brain Research,* **44,** 271–276.

Aggleton, J. P. (1993). The contribution of the amygdala to normal and abnormal emotional states. *Trends in Neurosciences,* **16,** 328–333.

Anderson, J. R., Montant, M., & Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioral Processes,* **37,** 47–55.

Baron-Cohen, S. (1994). How to build a baby that reads minds: Cognitive mechanisms in mindreading. *Current Psychology of Cognition,* **13,** 513–552.

Baylis, G. C., Rolls, E. T., & Leonard, C. M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex in the superior temporal sulcus of the monkey. *Brain Research,* **342,** 91–102.

Brothers, L., Ring, B., & Kling, A. (1990). Responses of neurons in the macaque amygdala to complex social stimuli. *Behavioral Brain Research,* **41,** 199–213.

Bruce, C., Desimone, R., & Gross, C. G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of Neurophysiology,* **46,** 369–384.

Butterworth, G., & Jarrett, N. (1991). What minds have in common is space: Spatial mechanisms serving joint visual attention in infancy. *International Journal of Behavioral Development,* **9,** 55–72.

Byrne, R. W. (1995). *The thinking ape: Evolutionary origins of intelligence.* New York: Oxford Univ. Press.

Byrne, R. W., & Whiten, A. (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans.* Oxford, UK: Clarendon Press.

Call, J., & Tomasselo, M. (1998). Distinguishing intentional from accidental actions in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Journal of Comparative Psychology,* **112,** 192–206.

Corkum, V., & Moore, C. (1994). Development of joint visual attention in infants. In C. Moore & P. Durnham (Eds.), *Joint attention: Its origin and role in development.* Hillsdale, NJ: Erlbaum. Pp. 61–85.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., and Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research,* **91,** 176–180.

Emery, N. J., Lorincz, E. N., Perrett, D. I., Oram, M. W., & Baker, C. I. (1997). Gaze following and joint attention in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology,* **111,** 286–293.

Emery, N. J., & Perrett, D. I. (1999). How can studies of monkey brain help us understand ''theory of mind'' and autism in humans? In S. Baron-Cohen, H. Tager-Flusberg, & D. J. Cohen (Eds.), *Understanding other minds 2: Perspectives from autism and cognitive neuroscience.* Oxford, UK: Oxford Univ. Press.

Gallese, V. (1996). Action recognition in the premotor cortex. *Brain,* **119,** 593–609.

Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences,* **2,** 493–501.

Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology,* **35,** 96–111.

Harries, M. H., & Perrett, D. I. (1991). Visual processing of faces in the temporal cortex: Physiological evidence for a modular organization and possible anatomical correlates. *Journal of Cognitive Neuroscience,* **3,** 9–24.

Hasselmo, M. E., Rolls, E. T., & Baylis, G. C. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research,* **32,** 203–218.

Hasselmo, M. E., Rolls, E. T., Baylis, G. C., & Nalwa, V. (1989). Object-centred encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey. *Experimental Brain Research,* **75,** 417–429.

Leekam, S., Baron-Cohen S., Perrett, D. I., Milders, M., & Brown, S. (1997). Eye-direction detection: A dissociation between geometric and joint attention skills in autism. *British Journal of Developmental Psychology,* **15,** 77–95.

Leonard C. M., Rolls, E. T., Wilson, F. A. W., and Baylis G. C. (1985). Neurons in the amygdala of the monkey with responses selective for faces. *Behavioral Brain Research,* **15,** 159–176.

Lorincz, E. N., Baker, C. I., Perrett, D. I., & Miall, R. C. (1998). Which visual cues monkeys use to follow attention: A study of social communication. *Society for Neuroscience Abstracts,* **24,** 1678.

Mistlin, A. J., & Perrett, D. I. (1990). Visual and somatosensory processing in the macaque temporal cortex: The role of ''expectation.'' *Experimental Brain Research,* **82,** 437–450.

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., & Dolan, R. J. (1996). A neural response within human amygdala differentiates between fearful and happy facial expressions. *Nature,* **383,** 812–815.

Oram, M. W., & Perrett D. I. (1994). Responses of anterior superior temporal polysensory (STPa) neurones to 'biological motion' stimuli. *Journal of Cognitive Neuroscience,* **6,** 99–116.

Oram, M. W., & Perrett, D. I. (1996). Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the macaque monkey. *Journal of Neurophysiology,* **76,** 109–129.

Oram, M. W., Perrett, D. I., & Hietanen, J. K. (1993). Directional tuning of motion-sensitive cells in the anterior superior temporal polysensory area of the macaque. *Experimental Brain Research,* **97,** 274–294.

Oram, M. W., Perrett, D. I., Wachsmuth, E., & Emery, N. J. (2000). Coding of limb, body-part and whole motion in the superior temporal sulcus (STS) of the macaque. Submitted.

Perrett, D. I. (1999). A cellular basis for reading minds from faces and actions. In M. Hauser &

M. Konishi (Eds.), *Behavioral and neural mechanisms of communication.* Cambridge, MA: MIT Press.

Perrett, D. I., Harries, M. H., Benson, P. J., Chitty, A. J., & Mistlin, A. J. (1990a). Retrieval of structure from rigid and biological motion: An analysis of the visual response of neurons in the macaque temporal cortex. In T. Troscianko & A. Blake (Eds), *AI and the eye.* Chichester: Wiley. Pp. 181–201.

Perrett, D. I., Mistlin, A. J., Harries, M. H., & Chitty, A. J. (1990b). Understanding the visual appearance and consequences of hand actions. In M. A. Goodale (Ed.), *Vision and action: The control of grasping.* Norwood, NJ: Ablex. Pp. 163–180.

Perrett, D. I., Harries, M. H., Bevan, R., Thomas, S. Benson, P. J., Mistlin, A. J., Chitty, A. J., Hietanen, J. K., & Ortega, J. E. (1989). Frameworks of analysis for the neural representation of animate objects and action. *Journal of Experimental Biology,* **146,** 87–114.

Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organisation and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London,* **335,** 23–30.

Perrett, D. I., Oram, M. W., Harries, M. H., Bevan, R., Hietanen, J. K., Benson, P. J., & Thomas, S. (1991). Viewer-centred and object-centred coding of heads in the macaque temporal cortex. *Experimental Brain Research,* **86,** 159–173.

Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental Brain Research,* **47,** 329–342.

Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Milner, A. D., & Jeeves, M. A. (1984). Neurones responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. *Human Neurobiology,* **3,** 197–208.

Perrett, D. I., Smith, P. A. J., Potter, D. D., Mistlin, A. J., Head, A. S., Milner, A. D., & Jeeves, M. A. 1985a. Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society, London B,* **223,** 293–317.

Perrett, D. I., Smith, P. A. J., Mistlin, A. J., Chitty, A. J., Head, A. S., Potter, D. D., Broenimann, R., Milner, A. D., & Jeeves, M. A. (1985b). Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey: A preliminary report. *Behavioural Brain Research,* **16,** 153–170.

Phillips, M. L., Young, A. W., Senior, C., Brammer, M., Andrew, C., Calder, A. J., Bullmore, E. T., Perrett, D. I., Rowland, D., Williams, S. C. R., Gray, J. A., and David, A. S. (1997). A specific neural substrate for perceiving facial expressions of disgust. *Nature,* **389,** 495–498.

Povinelli, D. J., & Preus, T. M. (1995). Theory of mind: Evolutionary history of a cognitive specialization. *Trends in Neuroscience,* **18,** 418–424.

Premack, D., & Woodruff, G. (1978). Does a chimpanzee have a theory of mind? *Behavioural and Brain Sciences,* **1,** 515–526.

Povinelli, D. J., & Preus, T. M. (1995). Theory of mind: Evolutionary history of a cognitive specialization. *Trends in Neuroscience,* **18,** 418–424.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research,* **3,** 131–141.

Rizzolatti, G., & Gentilucci, M. (1988). Motor and visual-motor functions of the premotor cortex. In P. Rakic & W. Singer (Eds.), *Neurobiology of neocortex.* New York: Wiley. Vol. 42.

Rolls, E. T. (1984). Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. *Human Neurobiology,* **3,** 209–222.

Rolls, E. T. (1986). Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the monkey. *Experimental Brain Research,* **65,** 38–48.

Rolls, E. T., & Baylis, C. G. (1986). Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the macaque monkey. *Experimental Brain Research,* **65,** 38–48.

Scaife, M., & Bruner, J. S. (1975). The capacity for joint visual attention in the infant. *Nature,* **253,** 265–266.

Tovee, M. J., Rolls, E. T., & Azzopardi, P. (1994). Translation invariance in the responses to faces of single neurons in the temporal visual areas of the alert macaque. *Journal of Neurophysiology,* **72,** 1049–1060.

Wachsmuth, E., Oram, M. W., & Perrett, D. I. (1994). Recognition of objects and their component parts: Responses of single units in the temporal cortex of the macaque. *Cerebral Cortex,* **5,** 509–522.

Wiener, S. G., & Levine, S. (1992). Behavioral and physiological responses of mother and infant squirrel monkeys to fearful stimuli. *Developmental Psychobiology,* **25,** 127–136.

Young, M. P., & Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. *Science,* **256,** 1327–1331.

Young, A. W., Aggleton, J. P. Hellawell, D. J., Johnson, M., Broks, P., & Hanley, J. R. 1995. Face processing impairments after amygdalectomy. *Brain,* **118,** 15–24.